GEOGRAPHIC DISTRIBUTION OF STINGLESS BEES AND ITS IMPLICATIONS (HYMENOPTERA: APIDAE)[1, 2]

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RECEIVED FOR PUBLICATION JUNE 15, 1962

Abstract Geographic distribution of stingless bees and the number of species per continent are given. South America is considered the center of origin and dispersion of stingless bees because it has: a) 183 species against 32 in Africa, 42 in Asia plus Indonesia West of the Wallace-Weber line, 20 in Australia, New Guinea, and the Solomon Islands; b) primitive species with n = 9 chromosomes etc; c) highly specialized species.
Possible migration of stingless bees since the Paleocene is studied. Their progress can be followed through six maps included in the paper.
The fossil *Meliponorytes succini* Tosi is considered close enough to *Meliponula bocandei* (Spinola) to justify joining them in one genus.
Meliponorytes devictus was re-studied and found to be a valid *Trigona*, close to *T. iridipennis* of the subgenus (*Tetragonula*) and renamed *Trigona* (*Tetragonula*) *devicta* (Cockerell).
Methods of dispersal in the stingless bees are briefly discussed.

Geographic distribution of meliponids is often cited in classes on evolution to exemplify discontinuity. This distribution can be seen on map 1. The construction of this map and calculation of the number of species cited in the next page were done with help of the following papers: Schwarz 1932, 1937, 1938, 1939, 1940, 1943, 1948; Moure 1944, 1946, 1950, 1960a, 1960b, 1961; Moure and Kerr 1950; Michener 1959, 1961; Rau 1943; Wille 1959; Pagden 1957; Sakagami 1959, 1960; Sakagami and Yoshikawa 1961; Cockerell 1921, 1934; Tosi 1896; Kerr 1948 and with the copy of the files of Prof. J. S. Moure deposited in this College.

Obviously this distribution is incomplete. Every expedition to Brazilian areas where few bee collections have been made reveals several new species. Some islands of Indonesia, such as Celebes, Flores, Timor and the Moluccas, present few, if any species of meliponids, indicating the need for more collections in these regions.

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1 This work was financed in part by the Rockefeller Foundation by the Brazilian Research Council (C. N., Pq.) and by a Grant of the U. S. Dept. of Agric. Agric. Res. Service, under Public Law 480.

2 Submitted for inclusion in the **Herbert Schwarz Memorial Volume** (1962) but delayed in publication due to lack of space, cf. **70** p. 214.

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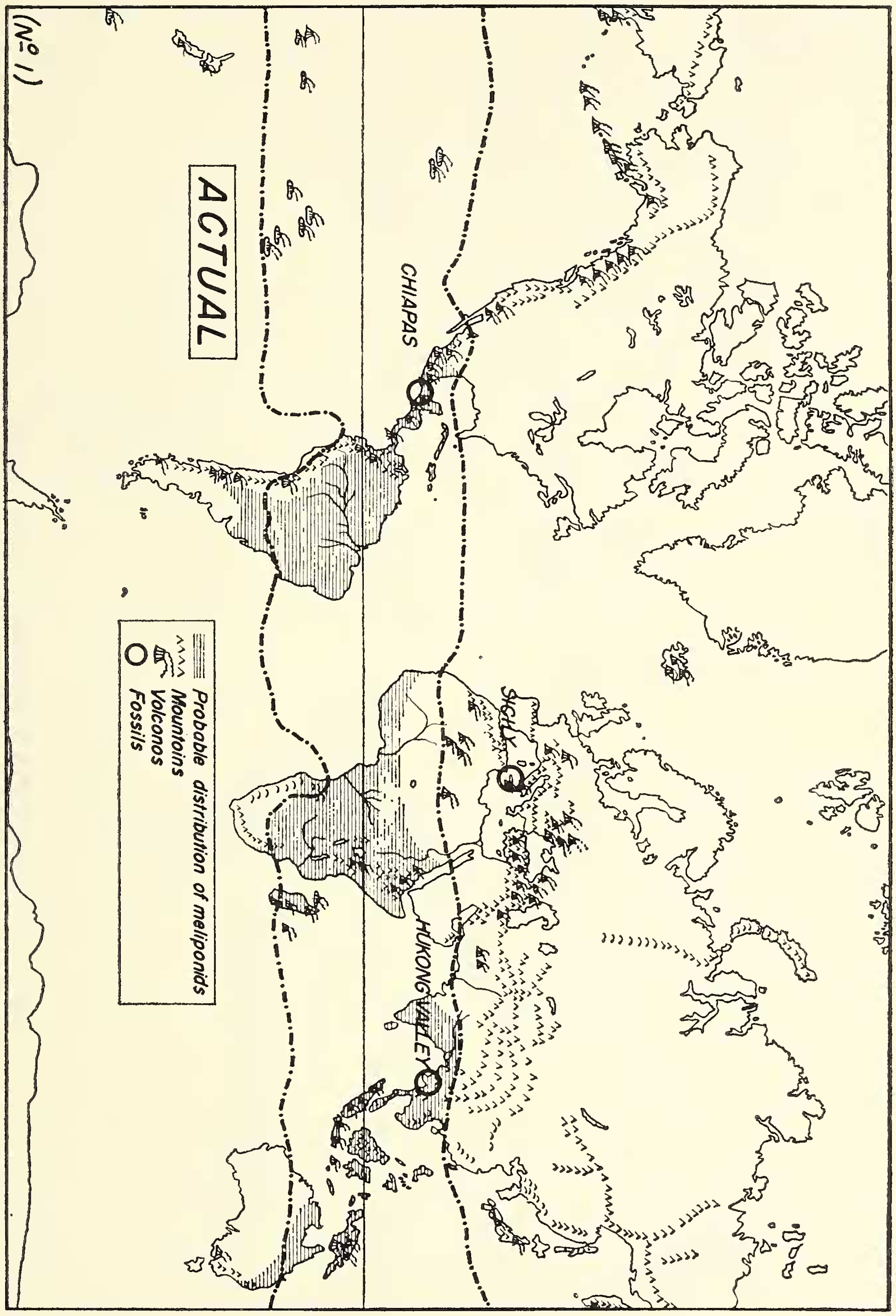
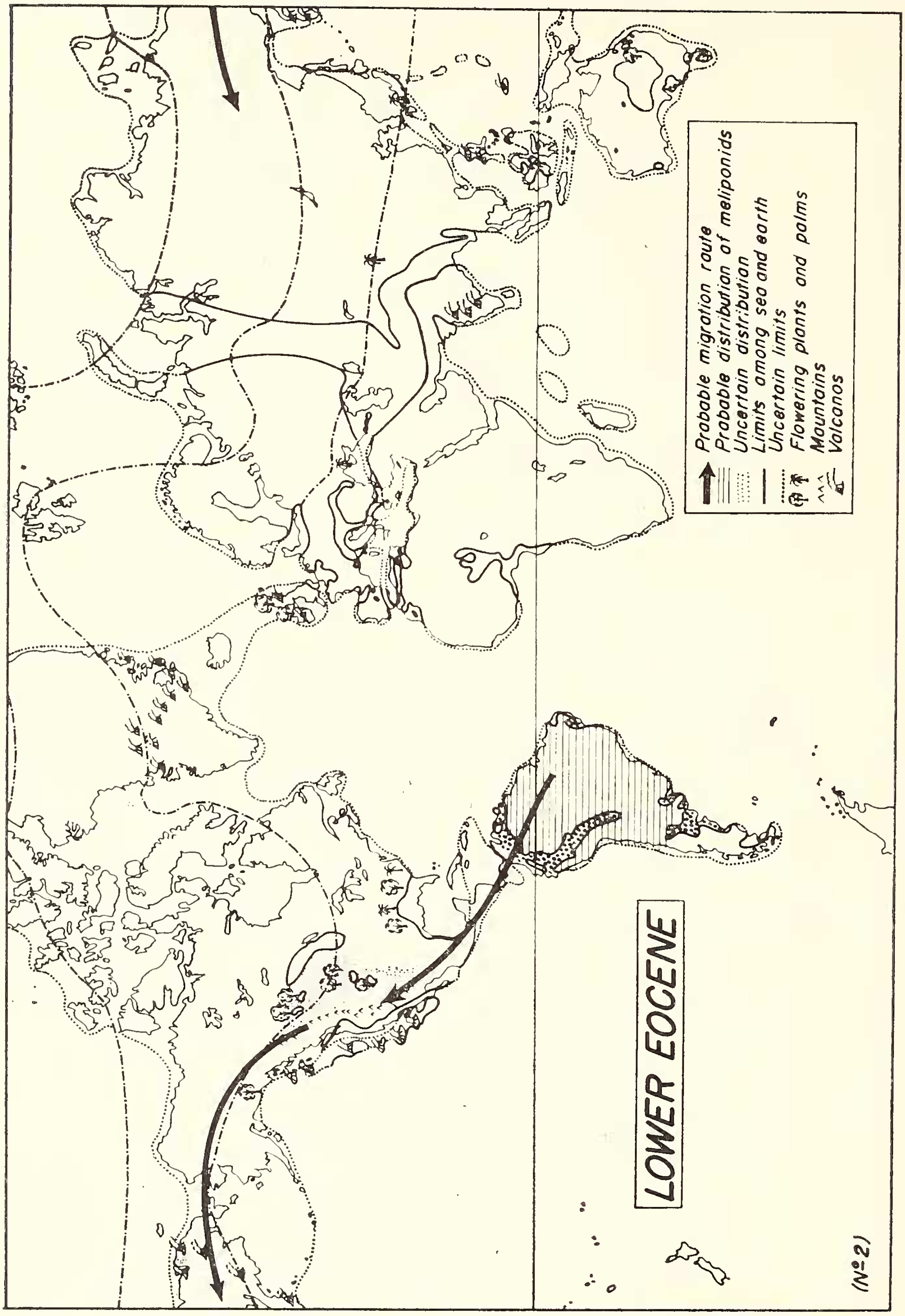


Map 1—Geographical distribution of stingless bees based upon references cited on p. 2 and sites where fossils were found.



Map 2—Possible invasion of North America and Asia by stingless bees in the Lower Eocene (about 65 million years ago). During Eocene connections and separations between South and North America existed. Palms are reasonable indications of climate tolerated by the bees. (Redrawn from map XXX of Termier and Termier, 1952.)

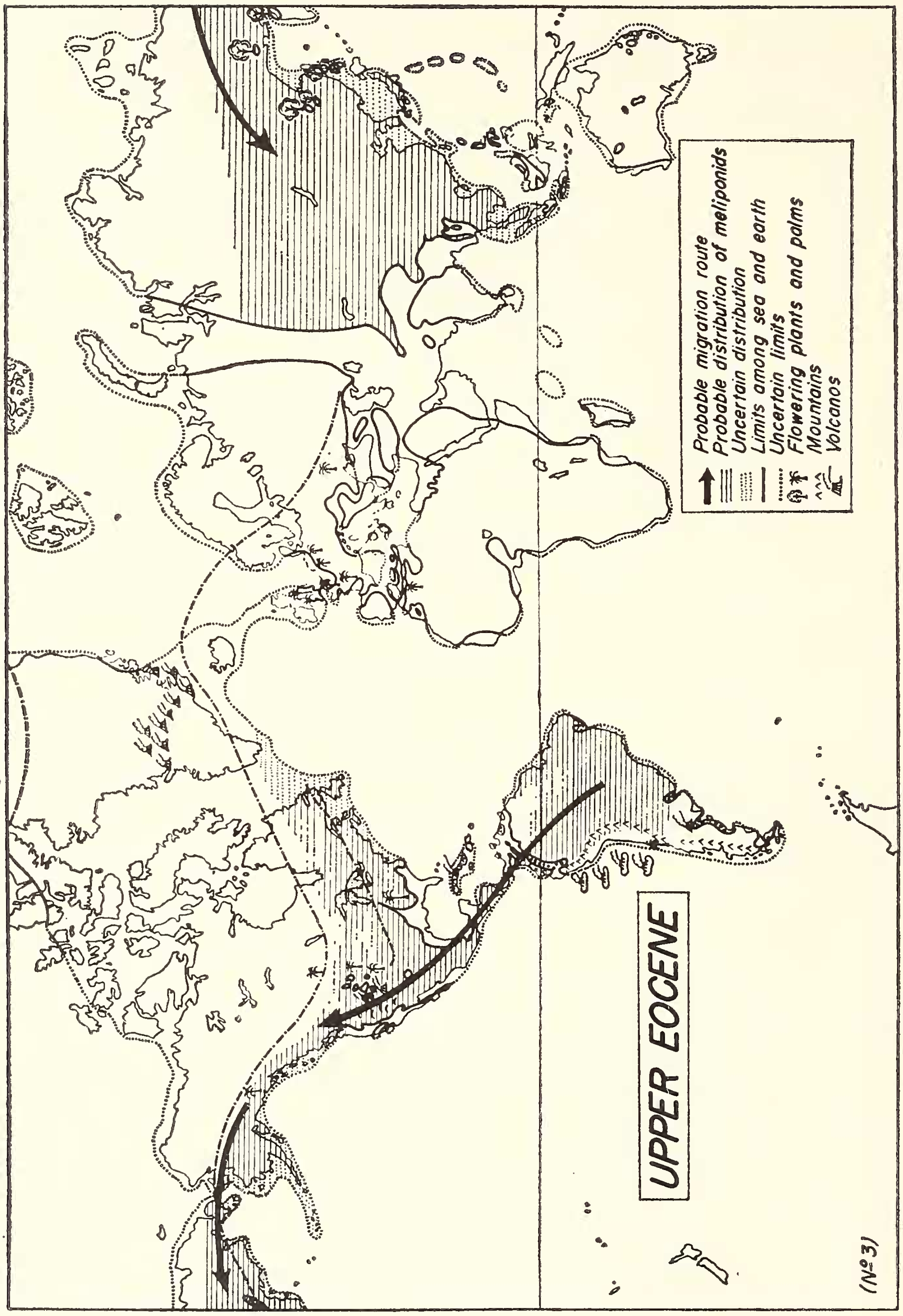
Areas of origin and speciation An important question is concerned with the region in which the meliponid group first developed and from which it radiated! Two facts that provide clues are, first, the degree of speciation in different regions and second, the primitiveness of species now existing.

The degree of speciation in the different regions can be judged from the present number of genera and species. Systematic criteria for genera in the meliponids are so variable, they have no biological basis unless treated objectively similar to treatment of Megachilidae by Michener and Sokal (1957). In this paper only the number of species will be used. The number of species found in the Americas is 183, in Africa 32, in Asia (including Sumatra, Java, Borneo, Celebes, Timor and Philippines) 42 species and in New Guinea, Australia and the Solomon islands 20 species, of which 7 species are shared with Asia. From this degree of speciation, the American continent, very likely South America (there are a total of 160 species in South America and 53 in Central America, 39 species being shared), seems to be the center of origin and, probably, the center of dispersion. The situation in Asia, Indonesia and Australia suggests that the bees entered Australia by way of Malaya, Borneo, and New Guinea. The small number of species in Celebes and the Moluccas may be due to deficient collections, as already mentioned.

The almost equal number of species in Africa and in Asia suggests that the group arrived in those regions at about the same time. Of the 14 Australian species, six are shared with New Guinea. Speciation is a process still active in stingless bees and cryptic species are often found as shown by Araujo and Kerr (1959) and Kerr (1960).

The primitiveness of existing species can be deduced by a comparative biological study. Consideration of nest structure, communication system, chromosome number, and the glandular system, indicate that the most primitive group is *Trigona* (*Frieseomelitta*). Besides having n = 9 chromosomes (Kerr, unpubl.) in *T.* (*F.*) *freiremaiai* (Moure), this subgenus makes tubes for pollen and pots for honey (a bombusoid character), and constructs cells grouped in clusters instead of combs. Another group with n = 9 is the genus *Melipona* (Kerr 1948). All other species examined have n = 18 or, in three cases, n = 17. Both *Melipona* and *Trigona* (*Frieseomelitta*) inhabit the American continent, suggesting that these are the most primitive bees.

In the American continent we find the most primitive and also the most evolved species, as well as a greater number of them, suggesting that they had more time to evolve. These facts strongly suggest South America as the place of origin of this group.



Map 3—Migration of meliponids in the Upper Eocene (about 55 million years ago). Tropical palms occur in Alaska, and the climate is temperate to 62°N (Schwarzbach, 1961). Lack of stingless bees in Oligocene Baltic amber suggests non-invasion of Europe in this period. (Redrawn from map XXXI of Termier and Termier, 1952.)

MIGRATION OF STINGLESS BEES THROUGH THE GEOLOGICAL TIMES The most ancient meliponid fossils, found in the Miocene, suggest that the group existed and was evolving at least during the two or three preceding geological periods.

The swarming system used by stingless bees limit their distance to 1000 meters from the hive. Therefore, the meliponids depend on land bridges for their migration and most of the principles used for the study of solitary insect distribution can not be used for these social bees.

The migration of stingless bees through geological times, taking in account their origin in South America, their swarming methods and the fossils, may have happened as follows:

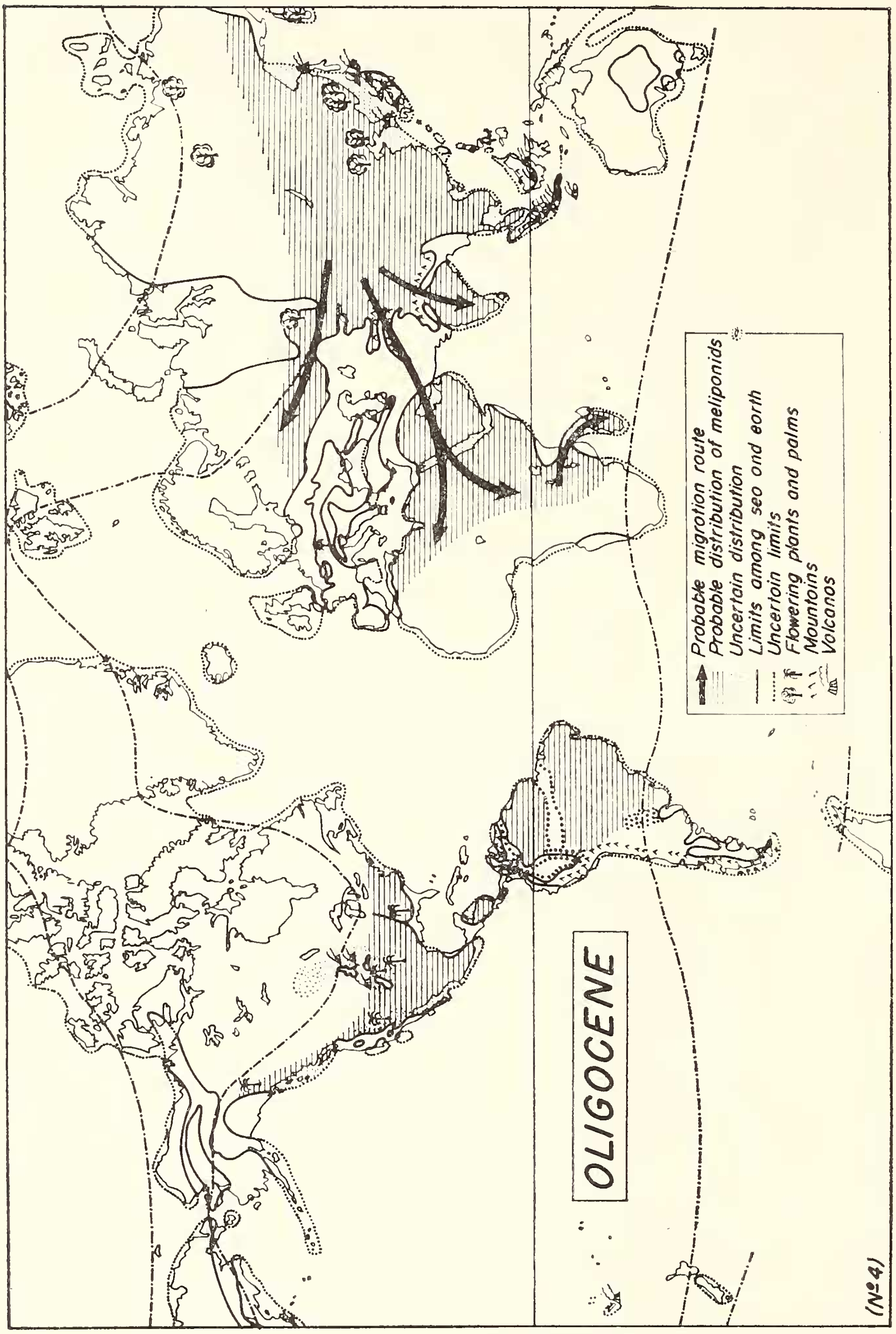
Map 2 (redrawn from map XXX of Termier and Termier 1952) shows the earth picture in the Paleocene. On this map two arrows show the possible invasion of North America and Asia by primitive meliponids. According to many paleogeographic experts this is the only geological period in all lower and medium tertiary in which a land invasion of Central and North America from South America could take place.

Map 3 (based on map XXXI of Termier and Termier 1952, corresponding to the Ypresian and Lutetian, or lower Eocene) shows the last migrations that might have continued to occur in the beginning of the lower Eocene. The majority of authors agree that by the medium and upper Eocene no further migration occurred between North and South America, this last one becoming completely isolated.

It is worth while to remember that the widely distributed Asiatic stingless bee *Trigona* (*Tetragonula*) *iridipennis* Smith, is also a primitive one as indicated by its communication (Lindauer 1956) and nest type (George 1934). This bee (already split in some subspecies) is known from India, Ceylon, Indochina, Malay Penninsula, Sumatra, Borneo, Penang, Java, Formosa, Philippines, Solomon Islands, Celebes, Caroline Islands, New Guinea, Australia, and possibly other Indonesian Islands. We believe that it had more time to become established in so many places because it is one of the most primitive.

In the Oligocene (Map 4), meliponid bees can invade Africa and, from Africa, Madagascar. Madagascar has four known species: two *T.* (*Liotrigona*) *bottegoi* (Magretti) and *T.* (*Liotrigona*) *bouyssoui* Vachal, are shared with the African continent.

Probably India received her first stingless bees in this period. Several African bees such as *Trigona* (*H.*) *araujoi* Michener, *T.* (*H.*) *braunsi* Kohl, *T.* (*H.*) *gribodoi* Magretti, *Meliponula bocandei* (Spinola), and *Lestrimelitta* (*Cleptotrigona*) *cubiceps* Friese have the cluster-like type of brood cell



Map 4—Invasion of Europe, India and Africa by the Oligocene (about 35 million years ago). Southern Europe has palms. Oligocene fossil of an amphisbaenid liazrd in Mongolia, common in Africa (Gilmore, 1943) suggests at least one connection between Africa and Eurasia in this period. Also, connections between Africa and Europe (Gibraltar and Sicily) existed. The climate in Somaliland was as hot as at present (Gill, 1961). (Redrawn from map XXXII of Termier and Termier, 1952.)

organization which is a primitive character. In fact *Meliponula bocandei* (Spinola 1853) has the most primitive type of blood food so far found: very dry and homogeneous, instead of being liquid with most of the pollen in the bottom of the alveolus and glandular food above. Due to the natural proximity it is likely that Asia and America exchanged species of stingless bees more easily than with Africa. In other words, African stingless bees have been more isolated. This may explain the evolution of types like *Dactylurina, Trigona* (*Axestotrigona*), etc. which are distinctive.

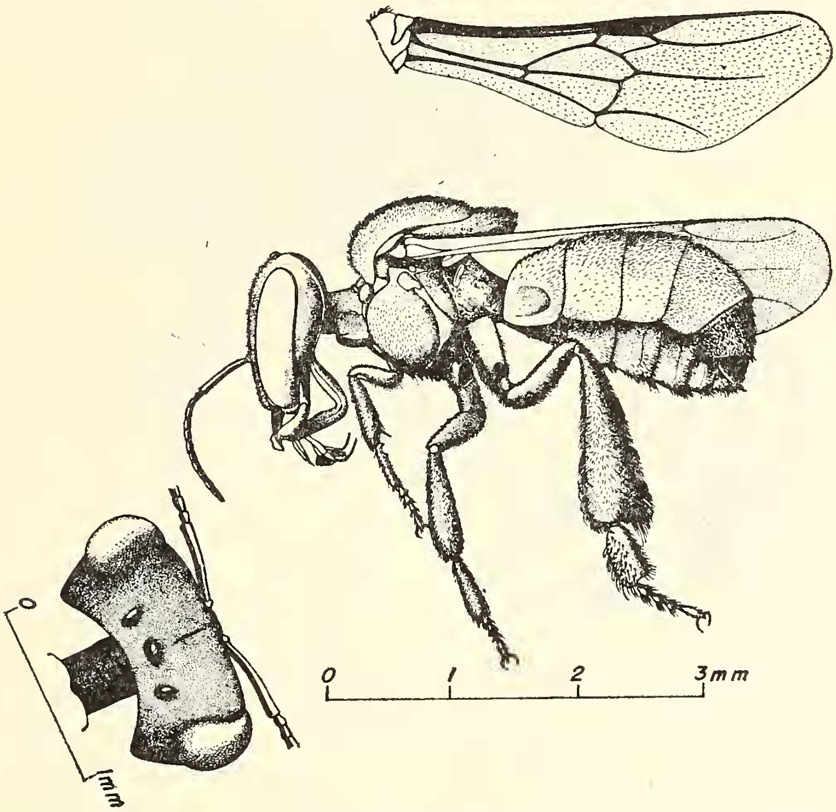


Fig. 1—*Meliponorytes succini* Tosi redrawn from Tosi (1896). Compare with Fig. 2. Lower left shows the head as seen from above. Possibly due to a slight inclination the wing (seen above bee) was drawn narrower than it is. The posterior part of the thorax is evidently wrong in this drawing and needs re-examination of the fossil bee.

It is possible, but not likely, that invasion of Europe had occurred by the Oligocene, since no meliponids were found among the bee fossils of the Baltic Oligocene.[1] This suggests that European invasion occurred

[1] When social bees inhabit a region their frequency is so large that most of the bee fossils of such an area are social bees. In Europe several fossils of *Apis* have been found:

Apis ambrusteri Zeuner (Upper Miocene, Bottingen, Swabia, Germany)

Apis dormitans (Heyden) (Oligocene)

Apis dormiens Zeuner and Manning (Upper Oligocene, Rott, Rhine Land)

Apis cuenoti Theobald (Oligocene, Cereste, France)

Apis scharmani Armbruster (Miocene, Randeck, Wurttemberg, Germany) either in the upper Oligocene or lower Miocene. (Map 4 was redrawn from Map XXXII of Termier and Termier 1952, omitting a possible African-American connection, questioned by these authors.)

The Miocene contains four fossils: *Meliponorytes sicula* Tosi, *Meliponorytes succini* Tosi, *Trigona* (*Tetragonula*) *devicta* (Cockerell) and *Trigona* (*Nogueirapis*) *silacea* Wille.

Meliponorytes sicula and *Meliponorytes succini*, studied by Tosi (1896)

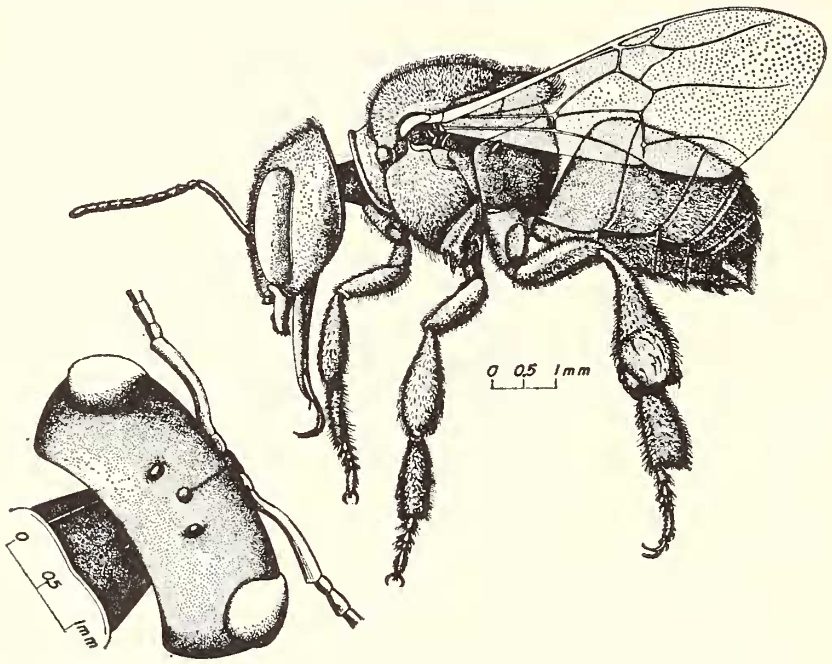


Fig. 2—*Meliponula bocandei* (Spinola) drawn in same position as *Meliponorytes* for easier comparison. Lower left: the head of *Meliponula* is seen from above.

are from Sicilian amber. The latter is similar to the African *Meliponula bocandei* and this would justify putting them in one genus but in different subgenera. But this decision should await more information of the fossil remains.[2] Their similarity is shown in figures 1, 2, 3 and 4. Figure 1 shows the outline of *Meliponorytes succini* Tosi, redrawn from Tosi (1896) and Figure 2 shows *Meliponula bocandei* (Spinola), drawn in the same position as Tosi did his fossil. The proportions among several parts of the body, the malar space, the scutellum, and especially the two denticles in the mandible closely resemble one another. The only real difference lies in the posterior part of the thorax, in the genal area and in the hind tibia. These differences may be due to the inferior drawing made by Tosi (the fore leg,

[2] In Oct. 1962 while visiting Bologna, Italy, Kerr learned that part of the collection of Sicilian amber was destroyed by a bomb during World War II. The Tosi fossils could not be studied.

the hind leg and the thorax have structural mistakes). Figure 3 shows a *Trigona* (*Nannotrigona*) *testaceicornis* (Lepeletier) and figure 4 shows a *Trigona* (*Scaptotrigona*) *xanthotricha* Moure. These two bees are considered of the same genus even by a systematist such as Prof. J. S. Moure, who wants to split the genus *Trigona* into more than twenty genera. The differences between these bees are of the same degree. Two facts strengthen our point of view: the geographic proximity of Sicily to the region where *Meliponula bocandei* exists, and the fact that the bees found by Wille (1959, 1961) and Cockerell in the Miocene are close to bees still existing in the same respective regions.

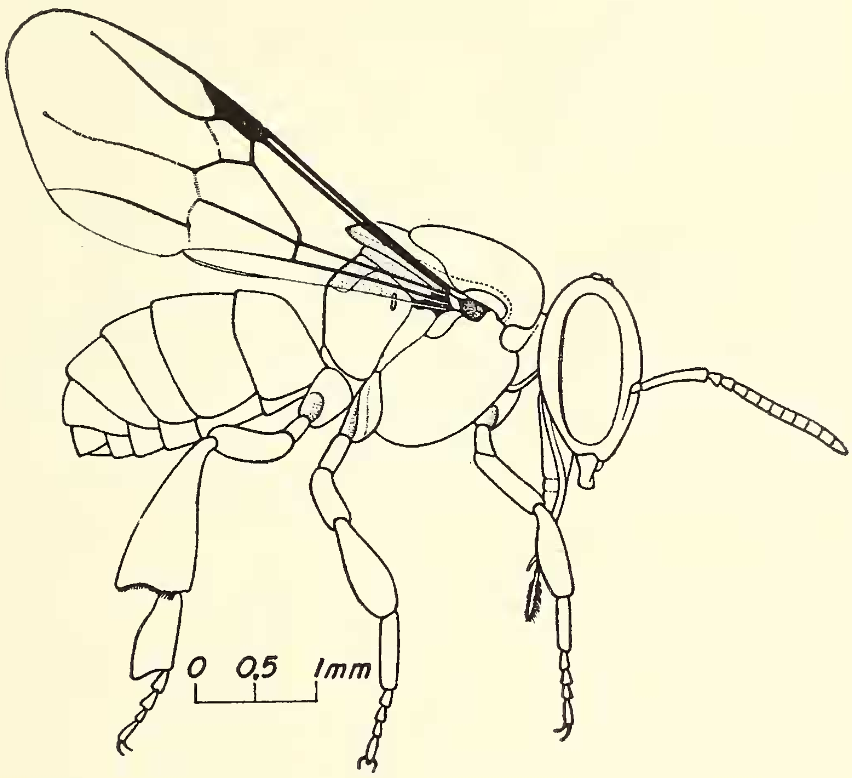


Fig. 3—*Trigona* (*Nannotrigona*) *testaceicornis* Lepeletier compare with Fig. 4.

The third fossil is *Trigona* (*Tetragonula*) *devicta* described by Cockerell (1921) from the Burmese amber as *Meliponorytes devictus*. The description of this bee shows clearly that it is a *Trigona agreeing* in all characters with the description given by Moure (1961) to the genus *Tetragonula*. Kerr examined this bee in the British Museum (fossil no. 20702) and considers it similar to the now existing *Trigona* (*Tetragonula*) *iridipennis* Smith. It deserves a different specific name due to its smaller size. Some measurements for comparison are the following (all measurements are in millimeters):

	devicta	*iridipennis*
Width of the head	1.350	1.550
Width of the eye	0.300	0.450
Ocellus diameter	0.095	0.120
Ocello-orbital distance	0.225	0.225
Length of the flagellum	1.000	1.150
Diameter 4th flagellum segment	0.100	0.130
Width of the thorax	1.275	1.577
Length anterior wing	2.500	3.250
Length hind tibia	0.925	1.475
Width of abdomen	1.075	1.350

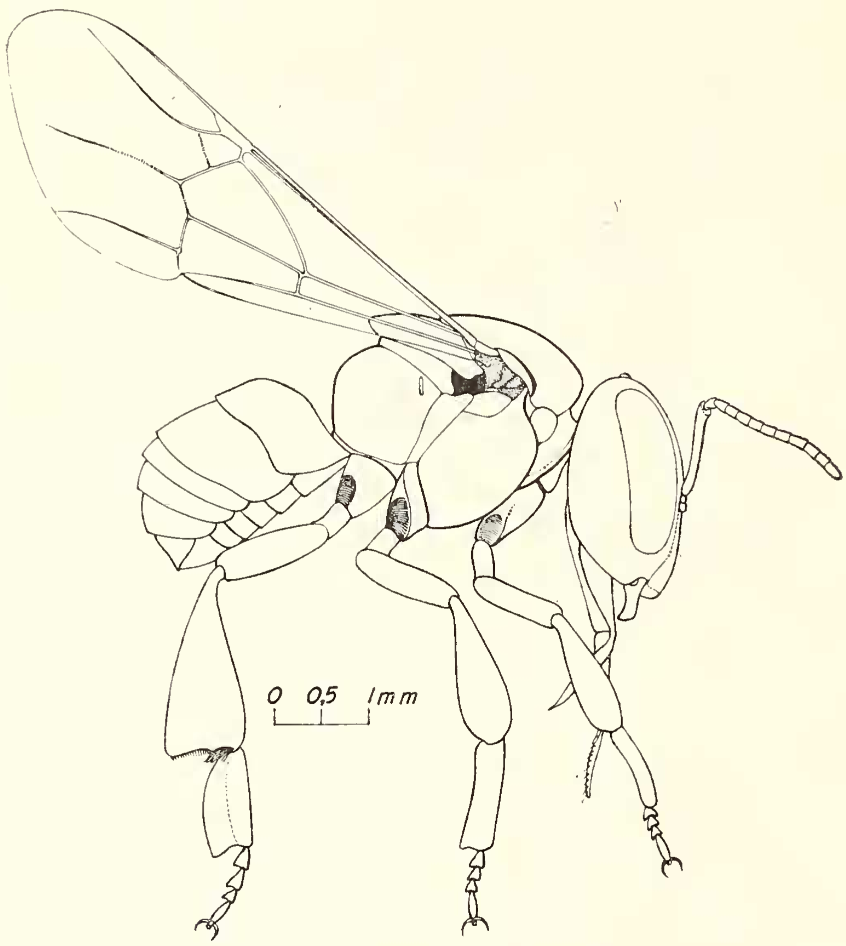


Fig. 4—*Trigona* (*Scaptotrigona*) *xanthotricha* Moure. Both this bee and *T.* (*N.*) *testaceicornis* are considered in the same genus. They differ more in proportion than bees from figures 1 and 2.

The *T.* (*T.*) *iridipennis* from which we took the measurements is from Burma (British Museum no. 2-94, Bingham Coll 96-3, from Tenasserim); no bee of this species was found as small as *T.* (*T.*) *devicta*.

Cockerell (1921) gives Gurnet Bay, Oligocene, as the geological period for all his Arthropod descriptions. He does not give similar information for *M. devictus* Cockerell. It seems more likely that *T.* (*T.*) *devicta* found in the Hukong Valley amber is from Miocene because in the Oligocene this area was a territory in formation still under the sea.

The fourth fossil is *Trigona* (*Nogueirapis*) *silacea* Wille, described by Wille (1959) from middle Miocene amber collected in San Pedro and Simojovel, both in Chiapas, Mexico and based upon eleven fossil bees. Interestingly there are at least two species, very close to this fossil, namely, *Trigona* (*Nogueirapis*) *butteli* Friese (a rare species from the upper Amazon basin) and *Trigona* (*Nogueirapis*) *mirandula* Cockerell (a rare species from Costa Rica), both considered by Wille (1961) as "living fossils". About the same geographical and morphological relation exist between *Trigona* (*Nogueirapis*) *silacea* Wille and *Trigona* (*N.*) *butteli* Friese, as between *Meliponorytes succini* (Tosi) and *Meliponula bocandei* (Spinola), and also, between the fossil *Trigona* (*Tetragonula*) *devicta* (Cockerell) and the living asiatic species *T.* (*T.*) *iridipennis* Smith. Obviously, these species are "living fossils". *T.* (*N.*) *silacea* thus, when *T.* (*N.*) *silacea* was fossilized, North and South America were already isolated, and thus shows that the migration had already occurred, as we suggested.

Map 5 (after map XXXIII of Termier and Termier 1952) shows where these fossils were found and the land connection shows the possibility of an invasion of the Indonesian islands to Australia. It is pertinent to recall that during this period several rodents left the continent and reached Australia and intermediate islands (Tate 1951; Simpson 1961). Australia has 14 species, 6 being in common with New Guinea. This suggests that New Guinea was the intermediate island in the colonization of Australia by stingless bees.

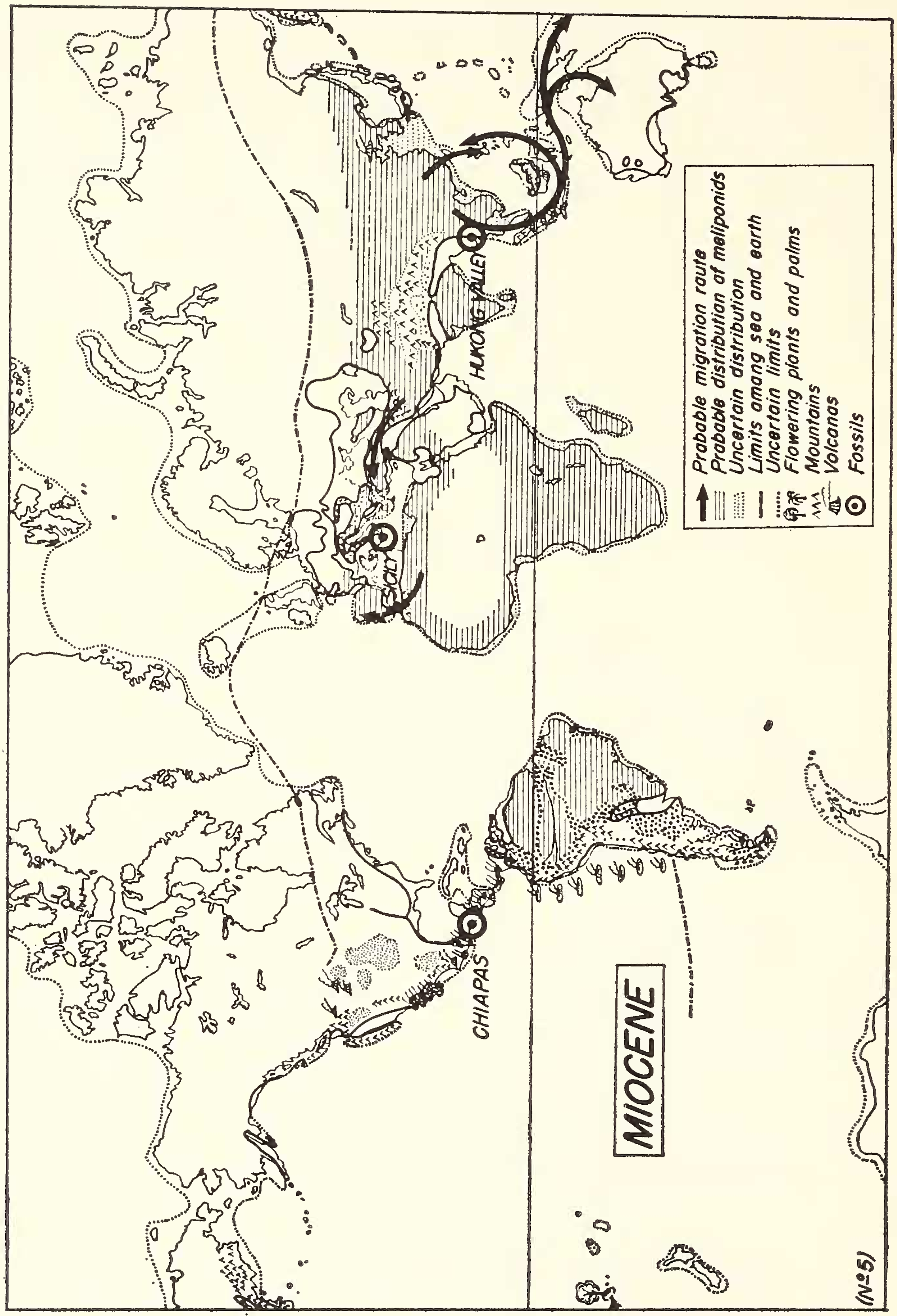
Map 6 (redrawn from map XXXV of Termier and Termier 1952), shows the Pleistocene (glacier time) that made the discontinuous distribution of stingless bees striking. Possibly we are now in a period in which meliponids are going north again, to reoccupy some of the lost positions.

Many of the Indonesian islands such as Sumatra, Borneo and Java, in their geological history had many connections with the continent. This explains why of the 42 meliponid species in that area, only one is autochthonous in Java, 6 autochthonous in Borneo and all the others shared with the continent.

Many invasions of African fauna to South America have been suggested (see Osborn, 1962) and the case of the stingless bees provide an example of the reverse invasion, as would be expected.

METHODS OF DISPERSION Biologically, migration of meliponids takes place under one of the following conditions:

swarming In meliponids this process sometimes takes more than a month.



Map 5—Meliponid fossils and migration in the Miocene (about 20 million years ago). Gradual invasion of Austromalayan archipelago is indicated by three-pointed arrow. Sicilian fossil indicates presence of stingless bees in Europe. South of Africa may be completely populated with stingless bees.

During this period the daughter colony maintains dependence on the mother colony for food, wax and workers (Nogueira-Neto, 1954). In species with small flight ranges a new colony can barely be established more than 50 meters from the mother colony. In species with long flight ranges (3 to 4 km.) a colony may be established as much as 1 km. distant. It is a well known fact that stingless bees do not like to fly over great masses of water and this is in contrast to some Bombus species that cross 2 or 3 kilometers of sea.

land connections The presence of good land connections in geological time would have made it possible for stingless bees to successfully cross present water areas because of the safety factors in their swarming system.

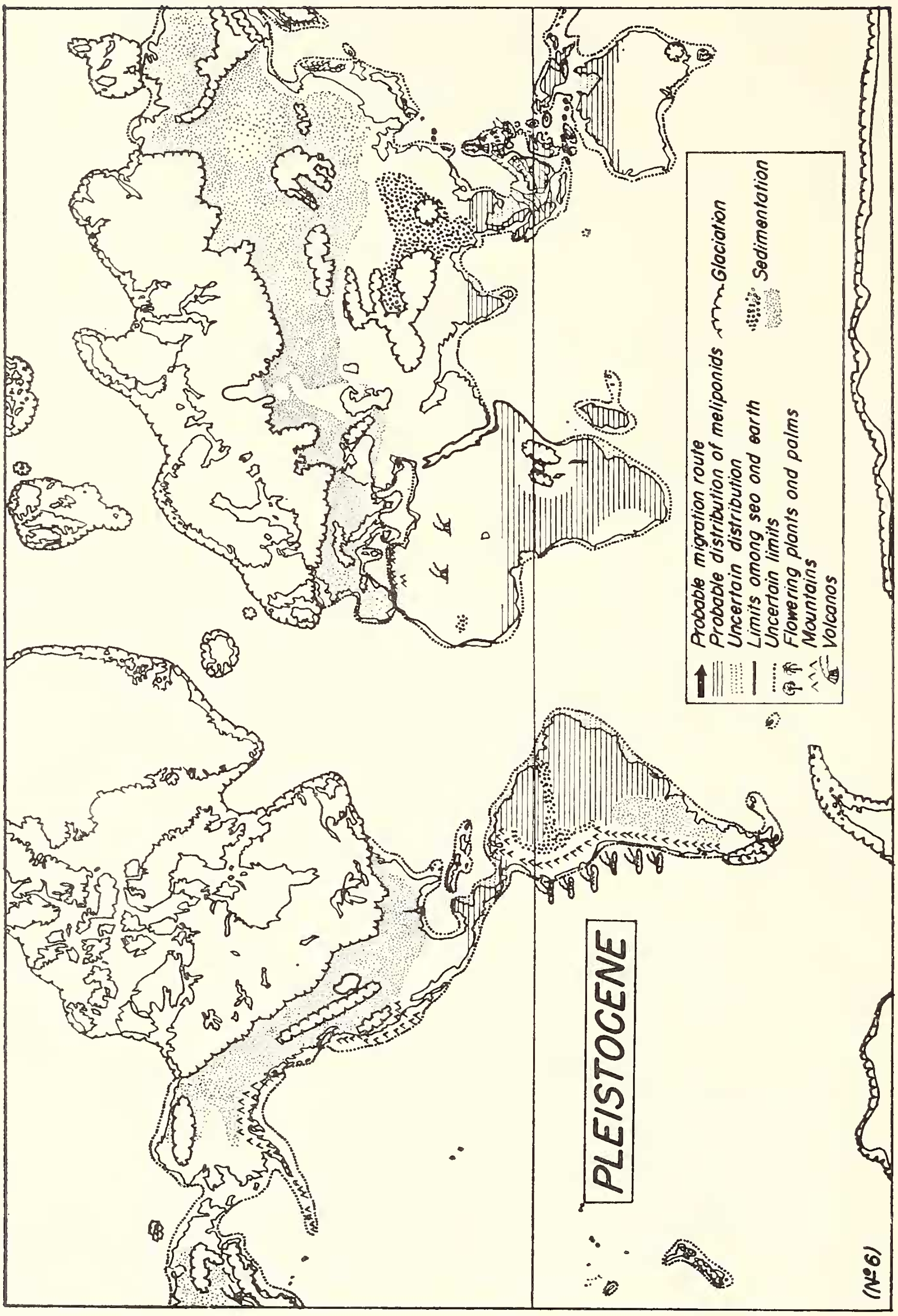
floating islands and **floating natural rafts** In the Amazon River, epecially after heavy rains, floating islands with an enormous number of animals and trees may be seen going down the river. In the same way a stingless bee colony, in due time, can cross a broad expanse of water. Many species can seal the nest entrance against water and enemies. Colonies of stingless bees have remained alive after a trip from northern and northeastern Brazil to São Paulo (southern Brazil) that lasted 20 to 40 days. This method could serve as a natural means of meliponid dispersal. However, the almost complete lack of stingless bees in the Caribbean Islands shows that this method is of no importance.

primitive men In view of the eagerness with which primitive men (Brazilian Indians) look and care for the treetrunk colonies it is easy to understand how distribution of some species in islands close to the continent or close to one another may have been effected by men in canoes. This may account for the existence of *Melipona beechei* in Yucatan, Mexico and in the islands of Cuba and Jamaica.

Acknowledgments

Our acknowledgments to: Prof. Dr. Henri Termier and Mme. Geneviève Termier for permission to reproduce their paleontological maps; Prof. J. S. Moure for giving our library a complete set of his files of systematic data on every species of meliponids described up to 1961; Dr. Gonzalo Halffter, Professor of Biogeography in the Escuela Nacional de Ciências Biologicas, Mexico; Dr. Alfredo Bjornberg, Professor of Geology in the Faculdade de Filosofia, Ciências e Letras de Rio Claro; Dr. L. Størmer, Professor of Paleontology in Oslo University, Norway, and Dr. Anatol Heintz, of the Paleontologisk Museum of Oslo, Norway, for help on geological information; Messrs. Masson and Cia., for permission to use the paleogeographical maps of Prof. H. Termier and G. Termier published by the press; Dr. C. D. Michener, Dr. Alvaro Wille, Prof. J. S. Moure, Dr. S. Sakagami, and Prof. C. C. Cruz who read this paper and gave valuable suggestions.

Dr. Paulo Nogueira-Neto gave us photocopies of the work of Tosi and the I.B.B.D. provided us with Cockerell's papers. Mr. J. Camargo made all the figures and maps.



Map 6—Disjunct distribution accomplished by glaciation during Pleistocene (1,000,000 to 15,000,000 years ago). Colonies subjected to cold climate died and meliponids were eliminated from north temperate regions. Some of this area was reoccupied after glaciation. (Redrawn from map XXXV of Termier and Termier, 1952.)

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